Revisionary Notes on the Phoxocephalidae (Amphipoda), with a Key to the Genera¹

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NOMENCLATURAL CHANGES deemed necessary by the writer are briefly discussed herein, including: (1) a new synonymy for the genus *Paraphoxus* Sars and a listing of useful specific criteria for that genus; (2) new combinations and new names in the genera *Paraphoxus*, *Heterophoxus* Shoemaker, and *Proharpinia* Schellenberg; (3) zoogeographical reasons for the provisional retention of the genus *Harpiniopsis* Stephensen; and (4) a new key to the existing genera of the Phoxocephalidae.

Initially, this study was a local faunistic problem in the marine basins off southern California (Hartman, 1955; J. L. Barnard, 1955). The wealth of materials collected in several hundred bottom samples by the research vessel, "Velero IV," necessitated an extensive review of phoxocephalid systematics in order to assign the many new species to appropriate genera. The present paper is confined only to a rearrangement of names and synonymies in the literature.

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PARAPHOXUS Sars, new synonymy

Paraphoxus Sars, 1893: 148. Pontharpinia Stebbing, 1897: 32. Parharpinia Stebbing, 1899: 207. Protophoxus K. H. Barnard, 1930: 335. Trichophoxus K. H. Barnard, 1930: 336. Metharpinia Schellenberg, 1931: 65.

Examination of specimens of *Paraphoxus* oculatus Sars from Norway, the type species of the genus, revealed a biarticulate first maxillary palp and not a uniarticulate condition as shown by Sars in 1893. Historically, the other genera in the above synonymy have been separated from *Paraphoxus* by the possession of a biarticulate palp; therefore, this distinction is no longer valid.

The genera *Parharpinia* and *Protophoxus* were already fused to *Pontharpinia* by Pirlot (1932). The genus *Trichophoxus* was based on the elongated fifth articles of the gnathopods, but the writer has found that this is not unusual in paraphoxids and of no generic value. *Metharpinia* was founded on species bearing narrowed rostrums (also characteristic of

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Phoxocephalidae — BARNARD

Trichophoxus) but the writer has found species which intergrade between the broad and narrow rostral types. However, it is useful to separate the two groups as subgenera, using the names *Paraphoxus* s.s. (broad rostrums) and *Trichophoxus* (narrow rostrums).

SPECIFIC CRITERIA IN THE GENUS PARAPHOXUS

Much of the apparent confusion in phoxocephalid systematics stems from the superficial lack of specific criteria. It is often the case that two species may appear quite similar with respect to head, gnathopods, peraeopods, uropods, and third epimera, which are the characters most useful systematically in other amphipods. Additional specific differences have been sought and one of the most important of these is the condition of the epistome. The presence of an acutely produced epistome in one of a pair of otherwise similar species has been most useful in calling attention to their distinctness and to a need for statistical measurement of other minor differences. Pontharpinia epistoma Shoemaker, 1938, was the first phoxocephalid described with a produced epistome. In the materials at hand are nine other new species bearing produced epistomes of varying extent, several of which are otherwise scarcely distinguishable from relatives in which the epistome lacks an anterior process.

Unfortunately, many of the existing specific descriptions of paraphoxids are practically useless and all species should be re-examined according to the following list of criteria. Due to the fact that seemingly minute differences may have specific value, drawings are far more useful than words.

The criteria deemed important by the writer and for which figures should be drawn are:

1. Dorsal shape of head and rostrum.

2. Size of eyes in both sexes in relation to size of head.

3. Shape of epistome from lateral view.

4. Presence or absence of a distal spine or claw on palp article 4 of the maxilliped.

5. Shape and size of articles 5 and 6 in both

pairs of gnathopods.

6. Stoutness of spination on article 5 of peraeopods 1 and 2.

7. Unusual features of the coxae.

8. Ornamentation and proportions of the articles of peraeopods 3, 4, and 5.

9. Configuration and armature of pleonal epimera 2 and 3.

10. Spination of uropods 1 and 2.

11. Proportions of uropod 3. The length of the inner ramus on the female is quite variable interspecifically, as is the length and shape of article 2 of the outer ramus.

12. Breadth, apical shape, and armature of telson.

13. Breadth and dorsal depression of body.

Paraphoxus milleri (Thorsteinson), new combination, new synonymy

Pontharpinia milleri Thorsteinson, 1941: 82. Pontharpinia longirostris Gurjanova, 1938: 263 (=Homonym, not Schellenberg, 1931).

Pontharpinia robusta Gurjanova, 1938: 262 (=Homonym, not Holmes, 1908).

A study of the variability of this species in eastern Pacific waters indicates that the names above should be fused. Both of the earlier names of Gurjanova are junior homonyms so that the only available name is *P. milleri*.

Paraphoxus obtusidens (Alderman), new combination, new synonymy

Pontharpinia obtusidens Alderman, 1936: 54. Pararpinia (sic) pontarpioides Gurjanova, 1953: 229.

The description and figures of the junior synonym represent one form of this variable northern Pacific species.

Paraphoxus sinuatus (K. H. Barnard), new combination, new synonymy

Parharpinia villosa, Schellenberg, 1931: 75 (not Haswell, 1879).

Parharpinia sinuata K. H. Barnard, 1932: 103-104, fig. 52.

The examination of the type of P. villosa, from Australia, by Dr. Keith Sheard and of Schellenberg's material, from South America, by the writer revealed several important differences in the South American species. The Parharpinia villosa of Schellenberg differs from the holotype by: (1) article 5 of gnathopod 1 shorter than 6, as opposed to longer than 6 in P. villosa; (2) article 6 of gnathopod 1 with parallel margins, as opposed to rounded in P. villosa; (3) article 4 of peraeopod 3 is only two thirds as wide as article 2 while it is fully as wide as article 2 in P. villosa; (4) article 2 of peraeopod 5 has the posterior edge with sparse and poorly setose serrations while in P. villosa it has numerous fine crenulations with long setae; (5) the peduncle of uropod 1 has numerous spines of strikingly different sizes on the inner and outer margins, as opposed to sparse similar spines on both margins in P. villosa; (6) the inner ramus of uropod 2 bears spines but lacks them in P. villosa.

Statistical analysis of large collections may show these differences to be of subspecific value only; in any case the South American specimens need nomenclatural segregation. This is provided by K. H. Barnard's name, *P. sinuata*, which by its description, figures, size, and geographic location is shown to be conspecific with Schellenberg's material.

Paraphoxus tattersalli, new species

Pontharpinia villosa, Tattersall, 1922: 4 (not Haswell, 1879a).

The clear figures published by Tattersall show striking divergence from the type of P. *villosa* which was examined by Dr. Sheard. Some of the many differences of P. *tattersalli* are: (1) gnathopods 1 and 2 differ in size greatly, while in P. *villosa* they are similar in size; (2) the short fifth articles of the gnathopods; (3) the very narrow plate of article 2 of peraeopod 5 compared with the very broad one in P. *villosa*; (4) article 4 of peraeopod 3 is half as wide as article 2, while in P. *villosa* it is fully as wide as article 2.

Paraphoxus stebbingi, new species

Pontharpinia pinguis, Stebbing, 1897: 33; Stebbing, 1906: 146 (in part); Stebbing, 1910: 635 (in part) (not Haswell, 1879*b*).

Stebbing's clear description and figures reveal several differences from the type of P. *pinguis* (Haswell), which was examined for the writer by Dr. Sheard. *Paraphoxus stebbingi* differs from *P. pinguis* by: (1) a minute cusp on the posteroventral corner of the third pleonal epimera, as opposed to a long, upturned cusp in *P. pinguis*, overlooked by Haswell in his description of the species; (2) the very elongated fifth articles of the gnathopods; (3) the narrow sixth articles of the gnathopods as opposed to the broad articles in Haswell's original drawing of *P. pinguis* (the sixth articles are missing on the type specimen of *P. pinguis*).

Heterophoxus oculatus (Holmes), new combination, new synonymy

Harpinia oculata Holmes, 1908: 521. Harpinia affinis Holmes, 1908: 523. Heterophoxus pennatus Shoemaker, 1925: 22.

The types of *H. oculata* and *H. affinis* in the U. S. National Museum were examined and found to be conspecific with *H. pennatus*. The name *oculatus* was chosen from Holmes' names on the bases of page priority, the better condition of the holotype, and the appropriateness of the name, referring to an animal with eyes.

Heterophoxus ophthalmicus (Schellenberg), new combination

Harpinia ophthalmica Schellenberg, 1925: 136.

Schellenberg's description is that of an heterophoxid, as shown by the presence of eyes, the ensiform process on the second antenna and the short fourth maxillipedal palp article bearing a long seta. However, on the basis of the description, the species cannot be differentiated from others in the genus *Heterophoxus*.

Proharpinia stephenseni (Schellenberg), new combination

Heterophoxus stephenseni Schellenberg, 1931: 73.

The type species of *Proharpinia* is *P. antipoda* Schellenberg, (1931: 80). Specimens of both *P. antipoda* and *H. stephenseni* were compared and found to be congeneric. The genus *Proharpinia* differs from the genus *Heterophoxus* only by: (1) the lack of an ensiform process on antenna 2; (2) the presence of a cusp on the lower anterior corner of the head. *Proharpinia stephenseni* may be separated from *P. antipoda* by: (1) the lack of teeth on article 2 of peraeopod 5; (2) a shorter tooth on the third pleonal epimera.

Probarpinia hurleyi, new species

- Harpinia obtusifrons, Chilton, 1909: 619 (in part) (not Stebbing, 1888); Stephensen, 1927: 306 (not Stebbing, 1888).
- Heterophoxus stephenseni, Hurley, 1954: 589 (not Schellenberg, 1931).

Some of Schellenberg's original material of H. stephenseni from South America (see previous species) and Hurley's specimens from New Zealand were compared and both were found to belong to the genus Proharpinia. However, the New Zealand specimens are a distinct species and differ from the P. stephenseni of South America by: (1) the presence of minute serrations on the posterior edge of peraeopod 5, article 2; (2) the longer tooth on the third pleonal epimera; (3) the stouter, longer spines on the telsonic apices; (4) the longer rostrum, smaller eyes of the female, and the smaller process on the lower anterior corner of the head; (5) the relatively longer sixth articles and more oblique palms of the gnathopods.

Chilton's specimens reported in 1909 (deposited at Canterbury University College) were examined and some were found to be *P. hurleyi* while the rest could not be identified. The reference of Stephensen (1927) was originally included as a part of the synonymy of *Heterophoxus stephenseni* by Schellenberg (1931) but it is clear from Stephensen's figures that the material belongs with *P. hurleyi*.

A ZOOGEOGRAPHIC NEED FOR THE PROVISIONAL USE OF THE NAME HARPINIOPSIS

The type species, *Harpiniopsis similis*, of this monotypic North Atlantic genus, described by Stephensen (1925) was submerged in the genus *Harpinia* by Gurjanova (1951).

The genus *Harpiniopsis* differs from *Harpinia* Boeck mainly by the very elongated male second antennae, a criterion generally true of all phoxocephalids, except for the specialized Harpinias. Although the writer deplores the use of secondary sexual criteria on which to base genera, he favors the retention of the name *Harpiniopsis* to designate a special group of harpiniids which may have important zoogeographic meaning.

The presence of only one species of *Harpiniopsis* in the rather well-explored northeastern Atlantic, compared with at least five undescribed species discovered by the writer in the eastern Pacific Ocean, is one example of the sparse representation of certain phoxocephalid genera in European Atlantic faunas. Another example of this is the presence of only one species of *Paraphoxus* in the northeastern Atlantic compared with several dozen species in the Pacific Ocean. On the other hand, the specialized genus *Harpinia*, which may have a *Harpiniopsis*-like ancestor, has many species in the European Atlantic but none in the tropical and temperate Pacific.

These facts lead to the suggestion that the Pacific Ocean, which is abundantly supplied with basic types of phoxocephalids such as *Paraphoxus* and *Harpiniopsis*, was the evolutionary center for the group. The only species of *Paraphoxus* in the northeastern Atlantic is also present in the northern Pacific, suggesting that it was the only one which successfully migrated to or survived in that part of the Atlantic. Only one species of *Harpiniopsis* survived in the north Atlantic, while its more specialized relative, *Harpinia*, probably evolved in and dominated the northeastern Atlantic phoxocephalid fauna. In light of the cold water habitats of the species of the genera in question, the migration pathway for these events undoubtedly occurred north of the American or Asian continents.

In the western Atlantic Ocean, along the warmer eastern shores of the Americas, is a *Paraphoxus* fauna closely allied and in some cases identical specifically with that in the tropical and semitropical eastern Pacific Ocean. It is of considerable interest that none of these paraphoxids has appeared in the warmer eastern Atlantic, suggesting difficulty or slowness of migration, or the inability to compete in the harpiniid-dominated eastern Atlantic.

Although these facts are meager they nevertheless point to a pressure of migration from the generalized and mixed phoxocephalid faunas of the northeastern Pacific Ocean to the more specialized, sparser, and geographically isolated faunas of the Atlantic Ocean.

It is advisable to retain the name *Harpiniopsis* for a group of species which are closely related to a theoretical precursor of the genus *Harpinia* and which, through distributional studies, may shed further light on the relationships of Pacific and Atlantic faunas.

KEY TO THE EXISTING GENERA OF PHOXOCEPHALIDAE³

- 3. Antenna 2, flagellum multiarticulate, gnathopods 1, 2 similar in size. Paraphoxus
- 3. Antenna 2, flagellum biarticulate, gnathopod 1 much larger than 2...Joubinella

4.	Mandible, molar bearing ridges and cusps
	Phoxocephalus
4.	Mandible, molar smooth or with a few
	spines
5.	Eyes present, maxillipedal palp article 3
	unproducedMetaphoxus
5.	Eyes absent, maxillipedal palp article 3
	produced conically Leptophoxus
6.	Eyes absent7
6.	Eyes present
	Head with dorsal crest, uropod 2 with
	apical ramal spines Pseudharpinia
7.	
	apical ramal spines
8.	Antenna 2 in male very short
	Harpinia
8.	Antenna 2 in male as long as body
	Harpiniopsis
9.	Antenna 2 with basal ensiform process
	Heterophoxus
9.	Antenna 2 lacks basal ensiform process
	Proharpinia

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⁸ The genus *Phoxocephalopsis* Schellenberg, 1931, was placed in the family Haustoriidae by K. H. Barnard, 1932, although it is intermediate between that family and the Phoxocephalidae.

Phoxocephalidae — BARNARD

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